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Empathy for positive and negative emotions in the gustatory cortex

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Anterior insula and adjacent frontal operculum (hereafter referred to as IFO) are active during exposure to tastants/odorants (particularly disgusting ones), and during the viewing of disgusted facial expressions. Together with lesion data, the IFO has thus been proposed to be crucial in processing disgust-related stimuli. Here, we examined IFO involvement in the processing of other people's gustatory emotions more generally by exposing participants to food-related disgusted, pleased and neutral facial expressions during functional magnetic resonance imaging (fMRI). We then exposed participants to pleasant, unpleasant and neutral tastants for the purpose of mapping their gustatory IFO. Finally, we associated participants' self reported empathy (measured using the Interpersonal Reactivity Index, IRI) with their IFO activation during the witnessing of others' gustatory emotions. We show that participants' empathy scores were predictive of their gustatory IFO activation while witnessing both the pleased and disgusted facial expression of others. While the IFO has been implicated in the processing of negative emotions of others and empathy for negative experiences like pain, our finding extends this concept to empathy for intense positive feelings, and provides empirical support for the view that the IFO contributes to empathy by mapping the bodily feelings of others onto the internal bodily states of the observer, in agreement with the putative interoceptive function of the IFO.

Keywords: Gustatory; Emotion; Empathy; Insula; Frontal operculum

Introduction

When we see the facial expressions of other individuals, we can often intuitively feel what they are feeling. The neural basis of this process has received intense interest. Based on the observations that the sight of other individuals' actions activate similar action programs in the observer and that the observation of other individuals' emotion of disgust activates regions of the brain involved in experiencing disgust, it has been proposed (Keysers et al., 2004; Gallese et al., 2004; Goldman and Sripada, 2005; Keysers and Gazzola, 2006) that feeling the emotions of other individuals involves the following: (a) observing the states of others activates representations of similar states in the observer; (b) these activations, which represent a form of simulation of the observed states, are sensed by a network of brain areas that represent bodily states; and (c) the sensed states are interpreted and attributed to the other individual, distinguishing them from the observer's own emotions.

The distinction between these subprocesses relates to one made in psychology. Young babies, while witnessing the distress of other individuals, often cry as if they were unable to distinguish their own distress from that of others (for a review see Singer et al., 2006). This phenomenon has been termed 'emotional contagion'. In contrast, while more mature individuals are not immune to emotional contagion, they are increasingly able to attribute the shared distress to the other individual, leading to an empathic *understanding* of the state of others (for reviews see Preston and de Waal, 2002; Gallese, 2003; Gallese et al., 2004; Decety and Jackson, 2004). Emotional understanding here refers to the conscious knowledge that someone else is currently experiencing a certain emotional state, as measured for instance by asking the observer to rate the emotional state of another individual (e.g. "how angry is that person from 0 to 6", as used in Adolphs et al., 2003), or a forced choice labelling task, as used in Calder et al. (2000). The processes of simulating and sensing the simulated state of others, hypothesised earlier (Gallese et al., 2004, Keysers and Gazzola, 2006), would be common to emotional contagion and empathic understanding (for reviews see Critchley, 2005; Adolphs, 2006). Thus only the third process of attribution, that enables an observer to associate his/her own simulated emotional state to that of the observed, differentiates early emotional contagion from more mature empathic understanding (for reviews see Frith and Frith, 1999, 2003; Singer, 2006). According to that view (Gallese et al., 2004, Keysers and Gazzola, 2006), mirroring/resonance and/or contagion are important prerequisites for empathic understanding.

At present, the quest to provide empirical evidence for the simulation theory has focused on providing evidence for the fact that the brain creates a simulation of the states of other individuals,

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with current evidence suggesting that the observation of the *negative* states of others triggers neural activations that resemble those associated with experiencing similar negative states. Both the observation of disgusted facial expressions and the experience of disgust activate the anterior insula and the adjacent frontal operculum, which will jointly be referred to as IFO (Phillips et al., 1997; Zald et al., 2002; Small et al., 2003; Wicker et al., 2003; Dapretto et al., 2006). The IFO is also activated when participants observe facial expressions of pain, know a loved one is in pain or experience pain themselves (Singer et al., 2004, 2006; Decety and Jackson, 2004; Botvinick et al., 2005; Jackson et al., 2006; Lamm et al., in press; Saarela et al., in press), with the participants that report having more empathic concern activating their IFO more strongly while aware of others' pain (Singer et al., 2004, 2006). In addition, lesions in the IFO impair both the experience of disgust (Adolphs et al., 2003) and the understanding of other people's disgust (i.e. impaired labelling of facial and vocal expressions of disgust) (Calder et al., 2000; Adolphs et al., 2003). Together these experiments converge to ascribe a pivotal role for the IFO in the network of brain areas that underpin the process of simulating observed states of others making the insula a likely neural structure important both for emotional contagion and empathic understanding.

The IFO has also been identified as essential for sensing one's own visceral bodily state (Craig et al., 2000; Critchley et al., 2001, 2002, 2003, 2004, 2005; for reviews see Damasio, 1996, Craig, 2002, 2003; Critchley, 2005), with people more able to sense their own heart beat showing stronger IFO responses (for a review see Critchley, 2005). Altogether, the IFO might therefore be engaged in two aspects that are key to simulation: the activation of simulated states, and the sensing of one's own state, be it simulated or experienced (Keysers and Gazzola, 2006). In addition, the IFO has been shown to have the pattern of efferent and afferent connections necessary for performing both tasks (Mesulam and Mufson, 1982a,b; Mufson and Mesulam, 1982).

Is the IFO confined to the processing of negative states, such as pain and disgust, or does it also process positive states, as long as the latter are associated with the visceral sensations that the IFO is thought to represent? The ingestion of pleasant foods and liquids, associated with such positive bodily states, provide a way to test this prediction that has, to our knowledge, so far not been explored. We therefore scanned participants while they viewed short movie clips of actors sipping from a cup and displaying either an intensely pleased, intensely disgusted or a neutral facial expression. Subsequently, we then scanned the same participants while ingesting pleasant (sucrose), unpleasant (quinine) and neutral (artificial saliva) solutions to map their gustatory IFO.

Individuals differ in their sensitivity to the feeling states of others, and these differences can be measured using self-report questionnaires, such as the Interpersonal Reactivity Index (IRI, Davis, 1980). Here, we measured participants' IRI scores and then searched for regions that respond more strongly to the gustatory experiences of others in participants with higher IRI scores. We restricted such a search to participants' functionally defined gustatory IFO. As argued previously (Singer et al., 2004, 2006; Gazzola et al., 2006) this approach searches for areas underpinning our inter-individual variation in transforming the states of other people into our own, a process thought to be essential for emotional contagion and empathic sharing.

Materials and methods

Participants and procedures

The institutional review board of the University Medical Center Groningen approved the study. Thirty-three healthy volunteers free from any known gustatory, olfactory, visual, neurological or psychiatric disorders gave written informed consent and participated in a screening and training sessions. Participants were screened for their taste sensitivity using labeled magnitude scaling (LMS) (Green et al., 1996), for the goal of excluding super/non tasters during the initial rating of the quinine and sucrose solutions as reported earlier (Small et al., 2003). We used quinine and sucrose for the taste screening with the participants reporting their perceived taste intensity on the LMS scale, ranging from 0 (barely detectable) to 100 (strongest imaginable). As we examine the influence of empathy on interindividual differences in brain activity, it is important to keep other sources of variance in check. In accordance with other studies (Small et al., 2003), we therefore restricted our experiments to participants in the normal range of tasting. Normal tasters were defined as those whose score for sucrose fell within the range of 15–75; while the normal tasting for quinine was define by scores ranging from 30 to 75. Normal tasting scores were obtained for all but 10 participants (9 non tasters and 1 super taster) who were excluded from fMRI. Of the remaining 23 participants that were scanned, two were excluded because of excessive movement, two for not being able to follow the taste and swallow instructions and one because of a vomiting spell. The final sample included in the analysis consisted of 18 right-handed healthy individuals (10 females; mean age 24, SD 2.64) as classified by the Edinburgh scale (Oldfield, 1971). Participants were questioned to ensure they were ignorant about the aim of the study before the event-related fMRI sessions (see Figs. 1 and 2).

Visual runs

Visual runs consisted of the observation of disgusted, pleased and neutral facial expressions (see Fig. 1). Actors were recruited from the Noord Nederlands toneel and the Jeugd theatre school, Groningen. They were asked to taste the content of a cup and express their resulting emotion in a naturally vivid manner (see Fig. 1). A separate group of 16 individuals rated the facial expressions of all the edited movies in terms of the intensity, naturalness and vividness of pleased, disgust, and the neutral expressions they recognized for each movie on a 7-point Likert scale. The 10 best clips for each emotional category in terms of the intensity, naturalness and vividness of expression of the emotions (as rated by the 16 individuals) for the three emotional conditions were selected for the final experiment. Each visual run contained all of the final selected 30 movie clips (3 s each, 10 movies per condition $\times$ 3 conditions) presented in a randomized event-related fashion with a red fixation cross between two movie clips.

Gustatory runs

Participants sampled and rated the intensity and pleasantness/unpleasantness of quinine (unpleasant taste) with a concentration of 1.0×10^{-3} M and sucrose (pleasant taste) with a concentration of 1.8×10^{-2} M as used previously (Small et al., 2003). The neutral taste consisted of artificial saliva (Saliva Orthana; Farmachemie BV Haarlem, the Netherlands; art no. 39.701.130) diluted with